

Review of the *Epeolus julliani* species group (Hymenoptera, Apidae, *Epeolus* Latreille, 1802), with descriptions of two new species

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Abstract

The nine species of the *Epeolus julliani* species group from the Palearctic region are reviewed. Two new species are described and illustrated: *Epeolus rasmonti* Astafurova & Proshchalykin, **sp. nov.** (Russia, Mongolia, China) and *E. kyzylkumicus* Astafurova, **sp. nov.** (Central Asia). *Epeolus julliani* Pérez, 1884 and *E. laticauda* Bischoff, 1930 are newly recorded from Kazakhstan and *E. seraxensis* Radoszkowski, 1893 is newly recorded from Kazakhstan and Tajikistan. An identification key for both sexes of all members of this species group is presented.

Keywords

Anthophila, Apiformes, cleptoparasites, Palearctic region, taxonomy

Introduction

In recent years, significant progress has been made towards a better understanding of the taxonomy of the species of *Epeolus* Latreille, 1802 from the Palearctic region, in particular Europe (Bogusch and Hadrava 2018; Le Divelec 2021), the Middle East and North Africa (Bogusch 2021), Turkey (Bogusch 2018), and Central Asia and Mongolia (Astafurova and Proshchalykin 2021a, b, c, 2022). In total, about 45 species

are now known from the Palaearctic. Based on specimens from several collections, the present work aims to complement these studies by providing a review of the *Epeolus julliani* species group.

The *julliani* species group includes *Epeolus fasciatus* Friese, 1895, *E. iranicus* Bogusch, 2021, *E. julliani* Pérez, 1884, *E. laticauda* Bischoff, 1930, *E. seraxensis* Radoszkowski, 1893, *E. siculus* Giordani Soika, 1944, and *E. transitorius* Eversmann, 1852.

Here, we add two new species to this group: *Epeolus rasmonti* Astafurova & Proshchalykin, sp. nov. from the East Palaearctic and *E. kyzylkumicus* Astafurova, sp. nov. from Central Asia.

This paper is meant as a further step towards a better documentation of the species of *Epeolus* and their distribution patterns in the wider Palaearctic region and adjacent areas. As previous years have shown, a greater number of undescribed species can be expected, particularly in the eastern, central and southern Palaearctic, where so far relatively little material has been available for study.

Materials and methods

The results presented in this paper are based on 257 specimens in the *Epeolus julliani* species group currently housed in the Zoological Institute, Russian Academy of Sciences (St. Petersburg, Russia, **ZISP**); Zoological Museum of the Moscow State University (Moscow, Russia, **ZMMU**); Federal Scientific Center of the East Asia Terrestrial Biodiversity, Far Eastern Branch of Russian Academy of Sciences (Vladivostok, Russia, **FSCV**); and Oberösterreichisches Landesmuseum, Biologiezentrum (Linz, Austria, **OLBL**).

The taxonomy and synonymy of species generally follow those of Bogusch and Hadrava (2018), except we regard *E. julliani* and *E. transitorius* as separate species, following Le Divelec (2021). Morphological terminology follows that of Michener (1944, 2007) and Engel (2001). The density of integumental punctures is described using the following formula: puncture diameter (in μm) / ratio of distance between punctures to average puncture diameter, e.g., 15–20 μm / 0.5–1.5.

Abbreviations **T** and **S** are used for metasomal tergum and metasomal sternum, respectively.

The species are listed alphabetically. We have used the following abbreviations for collectors: **AF** – A. Fateryga, **MP** – M. Proshchalykin; **SB** – S. Belokobylskij; **VG** – V. Gussakovskij, **VL** – V. Loktionov.

Specimens were studied with an Olympus SZ51 stereomicroscope and photographs were taken with a combination of stereomicroscope (Olympus SZX10) and digital camera (Olympus OM-D). Final images are stacked composites generated using Helicon Focus 7.7.4 Pro. All images were post-processed for contrast and brightness using Adobe Photoshop. New distributional records are noted with an asterisk (*).

The map was generated using an online tool for producing publication-quality point maps, SimpleMappr (Shorthouse 2010).

Taxonomy

Genus *Epeolus* Latreille, 1802

Epeolus Latreille, 1802: 427. Type species: *Apis variegata* Linnaeus, 1758, monobasic.

Epeolus julliani species group

Diagnosis. Labrum with apical margin straight and without medial tooth; apically or near apical margin (as opposed to medially, as in species in the *Epeolus variegatus* species group, or sub-apically, as in species in the *E. cruciger* species group) with two sharply carinate, triangular (as seen as lateral view) teeth (tubercles). Axilla large with short apical tooth (extending well beyond midlength of scutellum but not as far back as its posterior margin).

Species included. *Epeolus fasciatus* Friese, 1895, *E. iranicus* Bogusch, 2021, *E. julliani* Pérez, 1884, *E. kyzylkumicus* Astafurova, sp. nov., *E. laticauda* Bischoff, 1930, *E. rasmonti* Astafurova & Proshchalykin, sp. nov., *E. seraxensis* Radoszkowski, 1893, *E. siculus* Giordani Soika, 1944, *E. transitorius* Eversmann, 1852.

Remarks. Le Divelec (2021) also included *Epeolus flavociliatus* Friese, 1899 to this species group, but this species clearly differs from species *julliani* group by small (ill-defined) labral tubercles and elongate (longer than mesoscutellum) axillae. Additionally, the placement of *E. flavociliatus* in this group is not supported by recent phylogenetic studies (see Onuferko et al. 2019; Lim et al. 2022). Together with *E. priesneri* Bogusch, 2021, *E. subrufescens* Saunders, 1908, *E. warnckeii* Bogusch, 2018 and *E. ruficornis* Morawitz, 1875 this species rather belongs to another group.

Key to the species of the *E. julliani* species group

- | | | |
|---|--|----------------------------------|
| 1 | Anteromedial area of mesepisternum with deep depression (Fig. 8A, B)..... | 2 |
| – | Anteromedial area of mesepisternum normal, more or less flat..... | 3 |
| 2 | Subpleural signum positioned on a small elevated plate (Fig. 8C) and the mesepisternum lateral to anteromedian depression with a strong sharp carina (Fig. 8B) | <i>E. rasmonti</i> sp. nov. |
| – | Subpleural signum not elevated under mesepisternum; mesepisternum lateral to anteromedian depression with weak rounded corners (Fig. 8A) | |
| | | <i>E. transitorius</i> Eversmann |
| 3 | Female | 4 |
| – | Male | 10 |
| 4 | Apical bands of metasomal terga uninterrupted | 5 |
| – | Apical bands of metasomal terga interrupted medially (at least on T2–T4) | 6 |

- 5 Mesoscutum entirely reddish; F1 slightly longer than F2 (ca 1.5 vs 1.3–1.4 times as long as wide)..... *E. kyzylkumicus* sp. nov.
- Mesoscutum entirely black or largely black; F1 slightly shorter than F2 (ca 1.2 vs 1.3–1.4 times as long as wide) *E. seraxensis* Radoszkowski
- 6 Pubescence on S2 discs dense, obscuring integument..... *E. laticauda* Bischoff
- Pubescence on S2 discs sparse, sculpture of integument clearly visible..... 7
- 7 Mesoscutum and terga reddish..... *E. iranicus* Bogusch
- Mesoscutum and terga black. Mesoscutum sometimes reddish along margins but never predominantly reddish 8
- 8 F2 1.6–1.7 times longer than F3. Integument mostly black, labrum and axilla usually black. Mesepisternum sparsely punctate..... *E. fasciatus* Friese
- F2 slightly longer than F3. Integument with well developed red body coloration, labrum and axillae red. Mesepisternum densely punctate..... 9
- 9 Metasomal terga with bright yellow bands of tomentum; propodeum forms obtuse angle with mesoscutellum [known only from Sicily] *E. siculus* Giordani Soika
- Metasomal terga with pale-yellow or whitish bands of tomentum; propodeum forms right angle with mesoscutellum [widespread] *E. julliani* Pérez
- 10 Apical bands of metasomal terga interrupted medially (at least on T2–T4)..... 11
- Apical bands of metasomal terga uninterrupted 14
- 11 Metasomal terga reddish *E. iranicus* Bogusch
- Metasomal terga black 11
- 12 Apical bands of T1 uninterrupted..... *E. fasciatus* Friese
- Apical bands of T1 interrupted 13
- 13 Metasomal terga with yellowish bands of tomentum; propodeum forms obtuse angle with mesoscutellum [known only from Sicily] *E. siculus* Giordani Soika
- Metasomal terga with whitish bands of tomentum; propodeum forms right angle with mesoscutellum [widespread] *E. julliani* Pérez
- 14 Mesoscutum and terga reddish. Pygidium narrower, 1.05–1.1 times wider than long *E. kyzylkumicus* sp. nov.
- Mesoscutum and terga black or brownish. Pygidium wide, 1.4–1.7 times wider than long..... 15
- 15 Labral teeth positioned directly on apical margin. Hind basitarsus bordered by dense fringe of plumose setae. Pygidium wide, 1.6–1.7 times wider than long, apically distinctly bilobed. Lateral lobes of penis (best seen in dorsal view) small, triangular, extending to mid-length of penis valve (Fig. 9A, B, arrow) *E. seraxensis* Radoszkowski
- Labral teeth usually positioned near apical margin. Hind basitarsus bordered by sparse fringe of simple setae. Pygidium narrow, 1.4 times wider than long, apically slightly bilobed or rarely straight. Lateral lobes of penis (best seen in dorsal view) large, petal shaped, elongate, extending to tip of penis valve (Fig. 9I, J, arrow) *E. laticauda* Bischoff

***Epeolus fasciatus* Friese, 1895**

Epeolus fasciatus Friese, 1895: 208, ♀, ♂ (type locality: Hungary, Budapest [Pest]; Museum für Naturkunde, Berlin; Muséum National d'Histoire Naturelle, Paris; ZISP).

Material examined. HUNGARY, Pest [Budapest], 2.VII.1886 (1 ♂, syntype), Friese [ZISP].

Distribution. Southern and Central Europe, Turkey (Bogusch 2018).

***Epeolus iranicus* Bogusch, 2021**

Epeolus iranicus Bogusch, 2021: 52, ♀, ♂ (type locality: Kuhre-Sefid, Bazuft, Iran; OLBL).

Material examined. None.

Distribution. Iran (Bogusch, 2021).

***Epeolus julliani* Pérez, 1884**

Fig. 9E, F

Epeolus julliani Pérez, 1884: 318–322, ♀ (type locality: Marseille, France; Muséum National d'Histoire Naturelle, Paris).

Material examined. AUSTRIA, Wien, (1 ♀), coll. F. Morawitz, *transitorius* Eversm. [Morawitz det.] [ZISP]; AZERBAIJAN, Lenkoran, 28.VII.1930, (1 ♀), A. Shestakov [ZISP]; GEORGIA, Lagodehy, (1 ♀), coll. F. Morawitz [ZISP]; IRAN, Shaku, Elbrus Mts., VI.1914, (1 ♀), Kirichenko [ZISP]; Tularud, 11.V.1916, (1 ♂), B. Ilyin [ZISP]; Kerman Prov., 8 km N of Bordsir, 200 m, 29°55'N, 56°58'E, 6.VI.2010, (1 ♂), Mi. Halada (OLBL); MOLDOVA, Leovo, 25.VII.1913, (1 ♂), Chernavin [ZISP]; KAZAKHSTAN, Kokshetau Mts., 1. VII, 3.VIII.1958, (2 ♀), V. Rudolf [ZISP]; Aktobe, Berchogur [Birshoghyr], 26.VI.1910, (7 ♀, 3 ♂), L. Bubyer [ZISP]; RUSSIA, Dagestan Rep., 20 km W of Makhachkala, Sarykum, 23–24.V.2019, (1 ♂), MP, VL [FSCV]; CRIMEA, Mukhalatka, VII.1902, (1 ♀), N. Kuznetzov [ZISP]; Sevastopol, 28.VII.1916, (1 ♀), Pliginski [ZISP]; idem, 7.VII.2015, (1 ♀), V. Zhidkov [ZISP]; Tarkhankut, Atlesh, 29.VII.2008, (1 ♂), AF [ZISP]; Tarkhankut, Bolshoy Kastel, 25.VII.2015, (7 ♀), AF [ZISP]; idem, on *Jurinea stoechadifolia*, 8.VIII.2015, (1 ♀), V. Zhidkov [ZISP]; idem, 9.VIII.2020, (2 ♀), S. Ivanov [ZISP]; Tarkhankut, Kipchak, 16.IV.2016, (3 ♀, 1 ♂), V. Zhidkov [ZISP]; Tarkhankut, Dzhangul, 26.VII.2017, (3 ♀), AF [ZISP]; Feodossia, Karadag, 15.VI.2015, (1 ♀), AF [ZISP]; Lukull Cape, 8.VII.2015, (3 ♀), AF [ZISP]; near Sudak, 27.V.2016, (1 ♂), AF [ZISP]; Krasnodar Terr., Anapa, Bolshoy Utrish, 2.VII.2018, (1 ♀), AF [ZISP]; Orenburg Prov., Orenburg, (1 ♂), coll. F. Morawitz, *Epeolus transitorius* Eversm. [Morawitz det.] [ZISP]; SPAIN, Andalusia, 26.VI. (1 ♀, 1 ♂) [ZISP]; UKRAINE, Akkerman [=Bilhorod-Dnistrovskyi], (1 ♂), 21.VIII.1921, Petrovich [ZISP].

Remarks. The main differences between *Epeolus julliani* and *E. transitorius* are outlined by Le Divelec 2021, who removed the former from synonymy with the latter. Here, we describe the structure of the male genitalia (Table 1).

The integument coloration and variability are closest to *E. transitorius* (see below). Unlike *E. transitorius*, all studied female specimens of *E. julliani* have a sparsely pubescent or almost glabrous clypeus (vs on that is often obscured by dense tomentum), and the lower mesepisternum is always pubescent (vs often glabrous).

Distribution. North Africa, Middle East, Europe, Caucasus, Russia (south of European part, south Ural), *Kazakhstan, Iran (Bischoff 1930; Le Divelec 2021; current data).

Table 1. Main differences between species of the *Epeolus julliani* group.

	<i>seraxensis</i>	<i>iranicus</i> (according to Bogusch 2021)	<i>julliani</i> + <i>siculus</i>	<i>kyzylkumicus</i>	<i>laticauda</i>	<i>transitorius</i> + <i>rasmonti</i>
Both sexes						
Anteromedial area of mesepisternum	normal, more or less flat					with deep depression
Apical bands of metasomal terga	uninterrupted	interrupted medially on T2–T4	interrupted medially	uninterrupted	narrowly interrupted medially in female, uninterrupted in male	interrupted medially
Coloration of tergal discs	varies from brownish to reddish in female and from black to brownish in male	reddish	black	reddish	varies from dark brown to red-brown in female and from black to brownish in male	black
Female						
Length of flagellomeres (ratio L/W)	F1 little shorter than F2 (ca 1.2 vs 1.3–1.4); remaining flagellomeres distinctly longer than wide	F1 distinctly shorter than F2 (1.05–1.1 vs 1.35); remaining flagellomeres slightly longer than wide	F1 equal or little shorter than F2 (1.2 vs 1.2–1.3); remaining flagellomeres distinctly longer than wide	F1 little longer than F2 (ca 1.5 vs 1.3–1.4); remaining flagellomeres distinctly longer than wide	F1 little shorter than F2 (1.2–1.3 vs 1.4–1.5); remaining flagellomeres distinctly longer than wide	F1 distinctly shorter than F2 (ca 1.5 vs 1.0–1.1); remaining flagellomeres slightly longer than wide
Pubescence on S2 disc	dense, obscuring integument	sparse, sculpture of integument well-visible	sparse, sculpture of integument well-visible	moderate, almost obscuring integument	dense, obscuring integument	sparse, sculpture of integument well-visible
Male						
Lateral lobes of penis (dorsal view)	Small, triangular, extending mid-length of penis valve (Fig. 9C, D, arrow)	not studied	Small, petal shaped, extending mid-length of penis valve (Fig. 9E, F, arrow)	Medium sized, petal shaped, not extending tip of penis valve (Fig. 9C, D, arrow)	Large, petal shaped, elongate, extending tip of penis valve (Fig. 9G–J, arrow)	
Pygidium	very wide, 1.6–1.7 times wider than long, apically distinctly bilobed	1.3 times wider than long, apically rounded	1.25–1.35 times wider than long, apically rounded, sometimes slightly bilobed	1.05–1.1 times wider than long, apically rounded	1.4 times wider than long, apically slightly bilobed or rarely straight	1.1–1.2 times wider than long, apically rounded, sometimes slightly bilobed

***Epeolus kyzylkumicus* Astafurova, sp. nov.**

<https://zoobank.org/0DE6C379-8F69-40B6-9C77-BF90BFA4BD3E>

Figs 1–3, 8D, 9G, H

Material examined. Holotype: ♀, UZBEKISTAN, Kyzyl-kum [Kyzylkum desert], 10 km SW Arnasay [Lakes], 27.VIII.1979, Yu. Pesenko [ZISP]. **Paratypes:** 3 ♂, the same label as in the holotype; 1 ♀, KAZAKHSTAN, Perowsk [=Qyzylorda], Syr-Darja Geb., 17.VII.1909, W. Nikolsky [ZISP]; 1 ♀, TAJIKISTAN, Farap, NW Bukhara, 5.VII.1928, V. Gussakovskij [ZISP].

Diagnosis. This species is most similar to *Epeolus iranicus*, especially with regard to the extensive red integument coloration, but can be separated from it by the uninterrupted apical bands on the metasomal terga, dense pubescence of sterna, and longer antennae (flagellomeres distinctly longer than wide in both sexes vs slightly longer than wide in females and slightly shorter than wide in males of *E. iranicus*). The differences between *E. kyzylkumicus* sp. nov. and other species of the *julliani* group are outlined in Table 1.

Description. Female. Total body length 8.0 mm (Figs 1A, 2A); forewing length (without tegula) 6.0 mm.

Structure and sculpture: Head (Fig. 2B) 1.3 times as wide as long. Labrum (Fig. 2D) 1.65 (holotype) to 1.75 times (paratypes) as wide as long, angulated basally, rounded laterally and weakly concave medially, apical margin straight without medial tooth; close to apex (but not directly) with two well-visible teeth (tubercles); integument shiny, densely punctate (10–30 µm / confluent–2). Clypeus densely and finely punctate (10–15 µm / confluent–0.5), narrowly impunctate along apical margin. Frons with developed frontal keel. Frons and vertex areolate punctate (15–30 µm). Flagellomeres long, F1 1.5 times as long as wide, succeeding flagellomeres ca 1.3–1.4 times as long as wide. Mesoscutum and mesoscutellum coarsely and densely punctate (30–70 µm / confluent–0.5), small interspaces between punctures shiny and smooth. Axilla convex, apically with distinct short tooth. Mesoscutellum with deep medial longitudinal impression distinctly divided mesoscutellum on two slightly convex lobes; posterior margin scarcely extending over propodeum. Mesepisternum areolate-punctate (sculpture not visible under pubescence). Propodeal triangle shagreened. Metasomal terga densely and finely punctate (10–15 µm / 0.5–1), interspaces shiny and smooth; marginal zones (apical impressed area) wide, equal to length of discs. Pseudopygidial area triangular. Pygidial plate trapezoidal, apically truncate (Fig. 2C). Processes on sides of S6 normal, with short projections (Fig. 8D). Metasomal terga and sterna with punctures more or less equally dense.

Integument coloration: Body mostly reddish, but paraocular and genal areas, frons and vertex black.

Pubescence: Body with dense and mostly white tomentum (brownish only on medial part of tergal discs). Labrum with mixed thin and plumose setae. Face and genal area with dense tomentum obscuring integument, vertex with sparser and short

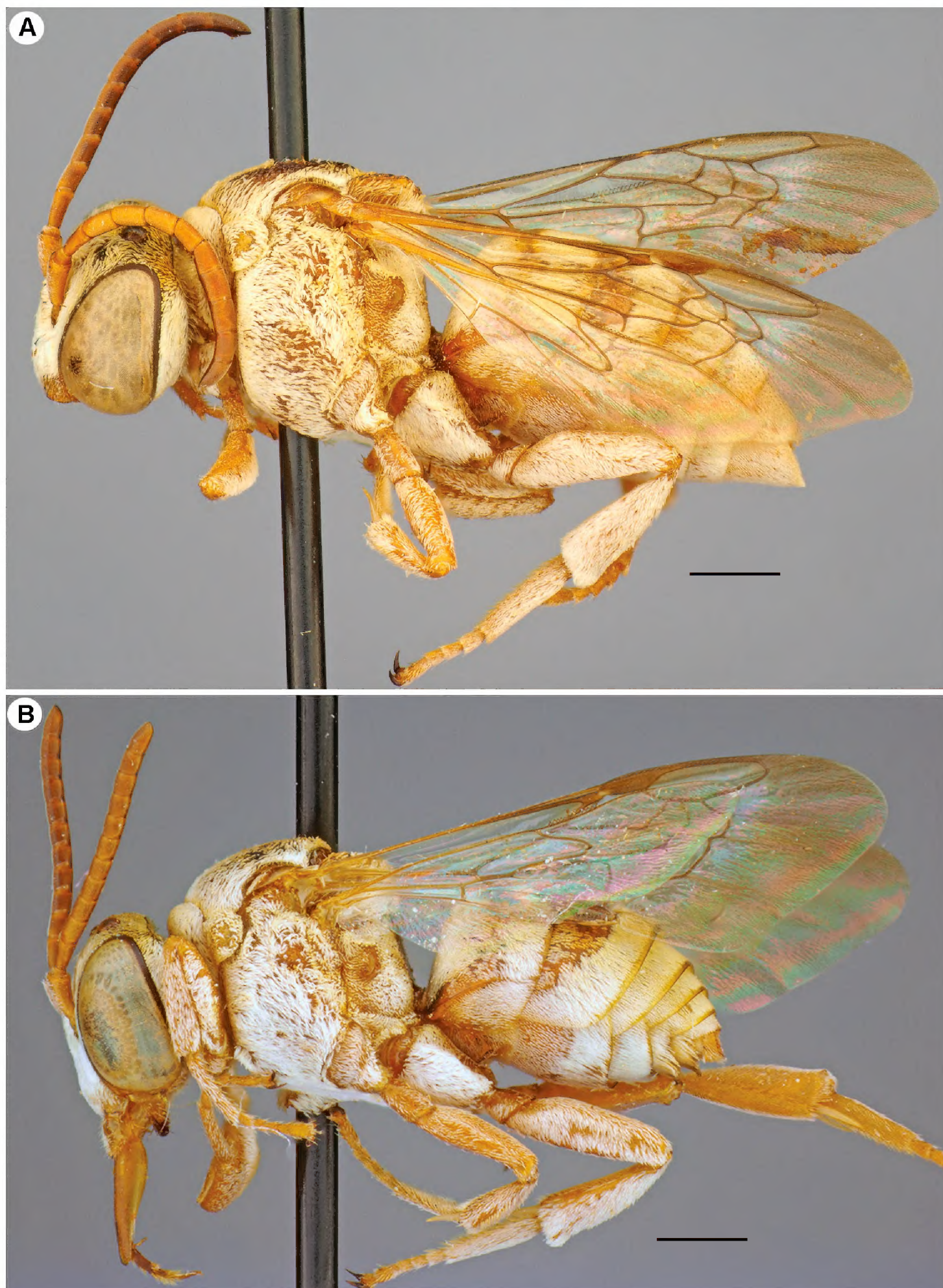


Figure 1. *Epeolus kyzylkumicus* Astafurova, sp. nov., holotype, female (**A**), paratype, male (**B**) **A, B** habitus, lateral view. Scale bars: 1.0 mm.

setae. Pronotum dorsally with tomentum obscuring integument. Mesoscutum with dense tomentum peripherally and with wide paramedial strips. Metanotal integument entirely obscured by tomentum. Lower and lateral parts of thorax and propodeum

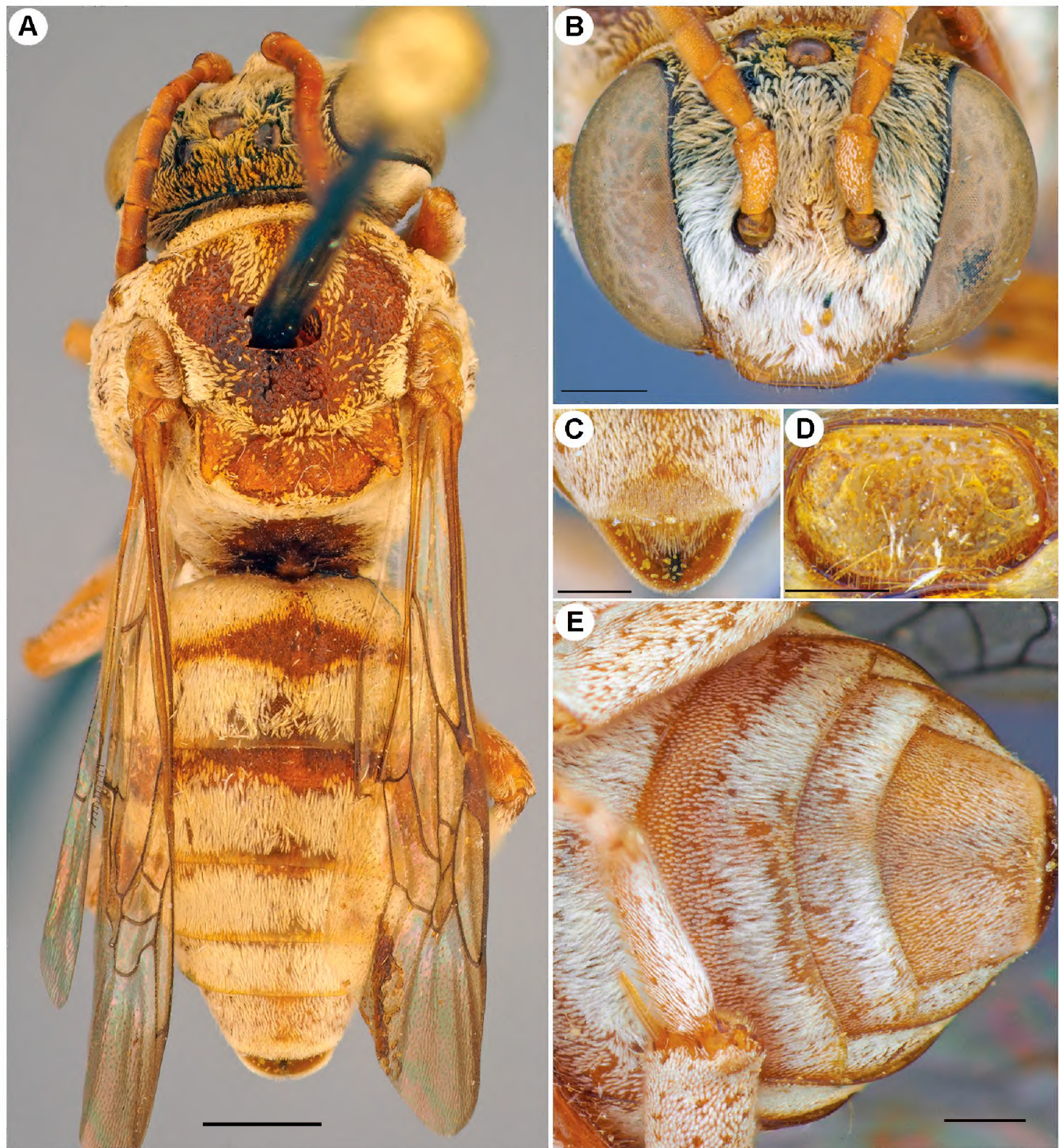


Figure 2. *Epeolus kyzylkumicus* Astafurova, sp. nov., holotype, female **A** habitus, dorsal view **B** head, frontal view **C** S6, ventral view **D** labrum, frontal view **E** metasoma, ventral view. Scale bars: 1.0 mm (**A**, **E**); 0.5 mm (**B**, **C**); 0.3 mm (**D**).

laterally entirely obscured by tomentum. Legs with dense tomentum. T1 with wide basal band of tomentum connected with apical band laterally; margins of T1–T4 with uninterrupted bands of tomentum. T1–T4 discs with tomentum dense and laterally similar to that on apical margins, but somewhat sparser and brownish medially. T5 entirely obscured by tomentum. Pseudopygidial area with golden pubescence. Sterna entirely obscured by tomentum, moderate on discs and distinctly denser and longer on margins (Fig. 2E).

Male. Structure, sculpture, coloration and pubescence are similar to those of the female (Figs 1B, 3A). Total body length 6.0–7.0 mm; forewing length (without tegula)

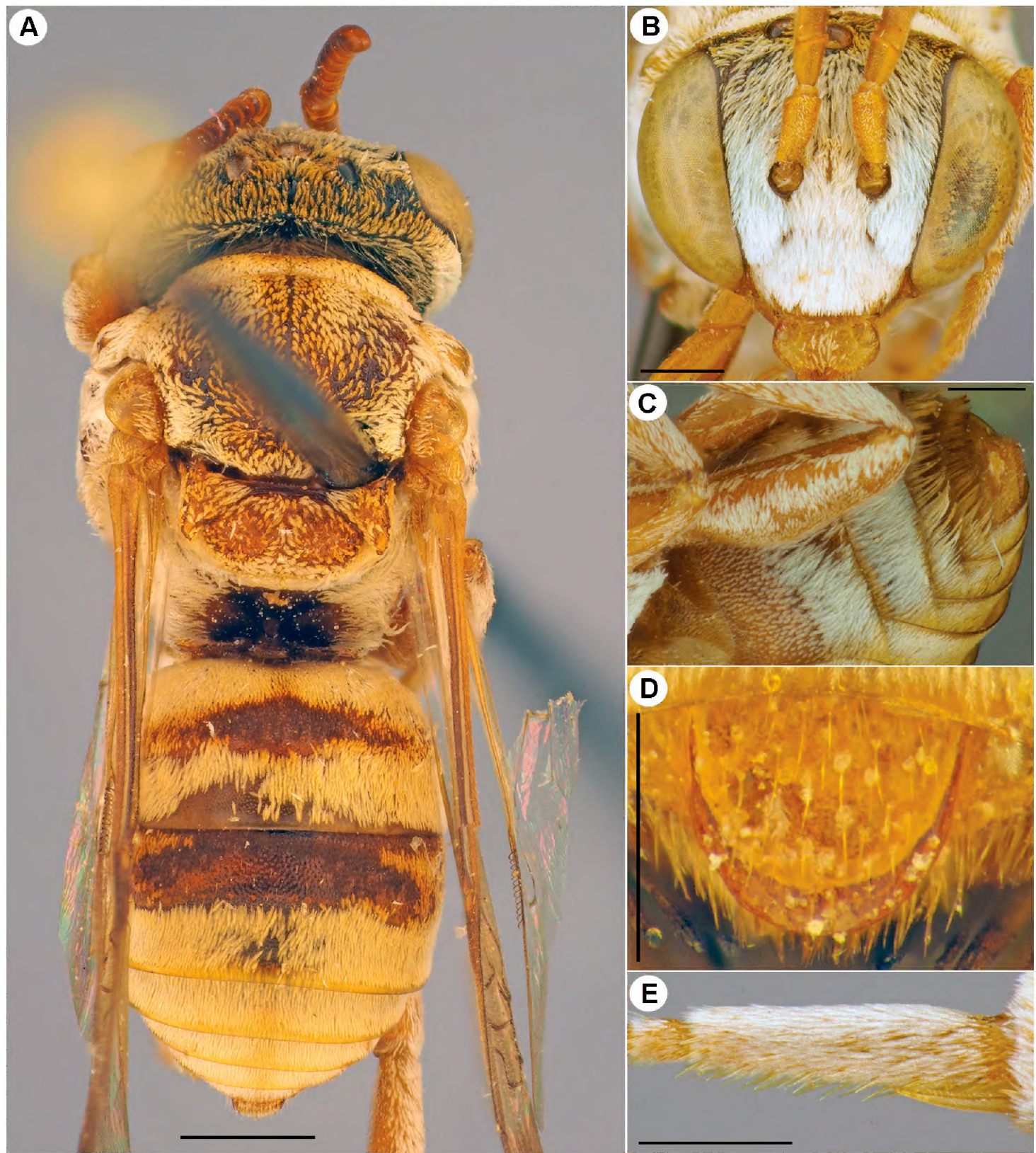


Figure 3. *Epeolus kyzylkumicus* Astafurova, sp. nov., paratype, male **A** habitus, dorsal view **B** head, frontal view **C** metasoma, ventral view **D** T7, dorsal view **E** hind basitarsus, dorsal view. Scale bars: 1.0 mm (**A**, **C**); 0.5 mm (**B**, **E**); 0.3 mm (**D**).

5.5 mm. Head (Fig. 3B) ca 1.2 times as wide as long. Labrum flatter and wider than in female, 1.9 times as wide as long. F1 ca 1.3 times as long as wide, succeeding flagellomeres ca 1.2 times as long as wide. Clypeus with dense tomentum obscuring integument. Mesoscutum entirely covered by plumose setae, denser peripherally and in anterior half. Hind basitarsus boarded by sparse fringe of pale short setae (Fig. 3E). Pygidial plate (T7) shiny, coarsely and densely punctate, 1.05–1.1 times wider than

long, slightly narrowed toward apex; apical margin rounded (Fig. 3D). Margins of S2 and S3 with dense uninterrupted white tomentum bands; S4 and S5 normal, with cream long setae (Fig. 3C). Genitalia as in Fig. 9C, D.

Etymology. The specific name “*kyzylkumikus*” is an adjective in the nominative singular and refers to the occurrence of this species in Kyzylkum desert of Central Asia.

Distribution. Kazakhstan (Qyzylorda Prov.), Kyrgyzstan, Tajikistan.

Epeolus laticauda Bischoff, 1930

Fig. 9I, J

Epeolus laticauda Bischoff, 1930: 13, ♂ (type locality: “Monda, Mongolei” [Mondy, Buryatia Republic, Russia]; Natural History Museum, Berlin).

Material examined. KAZAKHSTAN, Kulandy, Aral Sea, 13.VII.1900, (1 ♀, 1 ♂), L. Berg (ZMMU); Mergenevo, Ural River, 12.VII.1951, (1 ♀), Romadina [ZISP]; TAJIKISTAN, Kulyab, 7.VIII.1933, (2 ♀), V. Popov [ZISP]; Dzhili-Kul, Vakhsh River, 12.VI.1934, (1 ♀), VG [ZISP]; Kabadian, 2.VII.1934, (1 ♀, 2 ♂), VG; Ayvadh, 8.VIII.1934, (1 ♀), VG; Stalinabad [=Dushanbe], Botanical garden, 21.VII–8.VIII.1943, (9 ♀, 9 ♂), V. Popov [ZISP]; Kurgan-Tuybe, 14.VIII.1948, (1 ♀), V. Popov [ZISP]; TURKMENISTAN, Ashgabat, (1 ♀), coll. F. Morawitz, *transitorius* Eversm. [Morawitz det.] [ZISP]; Kara-Kala, 27.V.1953, (1 ♂), Steinberg [ZISP]; UZBEKISTAN, Farab, 31.V.1912, (1 ♀, 3 ♂), Golbek [ZISP]; Bukhara, 26.VI.1926, (1 ♀), V. Yakhontov [ZISP]; Khiva, 15.VI.1927, (6 ♀), VG [ZISP]; idem, 18–22.VI.1927, (1 ♀, 9 ♂), VG [ZISP]; Kattakurgan, 12.VII.1931, (1 ♀), VG [ZISP]; Dzhuma, 25–29.VI.1937, (15 ♀, 7 ♂), V. Popov [ZISP].

Distribution. Russia (Buryatia Rep.), *Kazakhstan, Tajikistan, Turkmenistan, Uzbekistan (Popov 1935, 1949, 1967; current data).

Variability. Labral tubercles in both sexes are positioned, typically, more or less close to the apical margin and rarely directly thereupon.

Females have well developed red body coloration. The labrum, clypeus, pronotal lobe, tegulae, mesepisternum, axillae, mesoscutellum, metanotum, legs, pygidial plate and sterna are always reddened. The antennae are mostly reddish, but with terminal flagellomeres usually brownish. The pronotum varies from reddish to partially black. The mesoscutum is mostly black, but red patterning sometimes also occurs laterally, or rarely it is almost entirely red-brownish. The propodeum varies from black to reddish. The metasomal terga vary from dark brown to red-brown with golden marginal zones; T5 is usually reddish.

Males are mostly black (excepting a red labrum, scape, pedicel, F1, pronotal lobe, tegulae, legs and pygidial plate). The clypeus is red (entirely or only in apical half). The mesepisternum, axillae and mesoscutellum are typically black, but sometimes can be partially or entirely red. The sterna vary from brownish to reddish. The pygidial plate apical margin is typically more or less bilobed, sometimes rather straight.

***Epeolus rasmonti* Astafurova & Proshchalykin, sp. nov.**<https://zoobank.org/B08677BE-9224-4C08-8E10-45B1F3DDAAAA>

Figs 4–7, 8B, C, 9G, H, 10

Material examined. Holotype: ♀, RUSSIA, Buryatia Republic, Gusinoe Lake, Baraty, 25.VII.2007, A. Lelej, M. Proshchalykin, V. Loktionov [ZISP]; **Paratypes:** 1 ♀, 1 ♂, the same label as in the holotype [FSCV/ZISP]; 6 ♀, 1 ♂, the same label as in the holotype, but 26.VII.2007 [FSCV/ZISP]; 1 ♂, Naushki, Selenga River, 30.VII.2007, A. Lelej, M. Proshchalykin, V. Loktionov [ZISP].

Additional material. CHINA, Beijing, park of the Summer Palace, 18.VIII.1954, (1 ♀), G. Bey-Bienko [ZISP]; MONGOLIA, Khutag, Selenga River, 25.VII.1975, (1 ♂), E. Narchuk [ZISP]; 200 km SEE of Baruun-Urt, Moltsoy Els, 1250 m, 27.VII.2007, (3 ♀, 14 ♂), M. Kadlecova, M. Halada, P. Tymer [OLBL]; 100 km NE of Ondorkhaan, Kerulen River, 970 m, 22.VII.2007, (3 ♂), M. Kadlecova [OLBL]; 100 km W Choibalsan, 820 m, 23.VII.2007, (1 ♂), M. Halada [OLBL]; 15 km W Choibalsan, Kerulen River, 770 m, 24.VII.2007, (1 ♂), M. Halada [OLBL].

Diagnosis. This species is most similar to *Epeolus transitorius*, with which it uniquely shares a deep depression in the anteromedian area of the mesepisternum, but can be separated from it by the position of the subpleural signum on a small elevated plate (Fig. 8C) and the presence of a strong, sharp carina on the mesepisternum lateral to the anteromedian depression (Fig. 8B) (vs weak rounded corners, Fig. 8A). The differences between *Epeolus rasmonti* sp. nov., *E. transitorius* and other species of the *julliani* group are outlined in Table 1.

Description. Female. Total body length 7.0–9.0 mm (Figs 4, 5A); forewing length (without tegula) 6.0–7.0 mm.

Structure and sculpture: Head (Fig. 5B) 1.3 times as wide as long. Labrum (Fig. 5C) 1.55 times as wide as long, more or less rounded basally and laterally, weakly concave medially, apical margin straight without medial tooth; apically with two well-visible carina-shaped teeth (tubercles); integument shiny, areolate punctate (10–30 µm). Clypeus densely and finely punctate (10–15 µm / confluent–0.5), narrowly impunctate along apical margin. Frons with developed frontal keel. Frons and vertex coarsely and areolate punctate (30–40 µm). F1 long, ca 1.5 times as long as wide, F2 distinctly shorter than F1 (1.0–1.1 times as long as wide), succeeding flagellomeres slightly longer than wide (ca 1.2 times). Mesoscutum and mesoscutellum coarsely and mostly areolate punctate (30–70 µm), a few small interspaces between punctures shiny and smooth. Axilla slightly convex laterally, apically with distinct short tooth. Mesoscutellum with shallow medial longitudinal impression; posterior margin scarcely extending over propodeum. Mesepisternum areolate punctate on upper half and with dull, delicately shagreened interspaces on lower part; anteromedian area with deep depression, laterally from anteromedian depression with strong sharp carina (Fig. 8B). Propodeal triangle shagreened. Metasomal terga densely and finely punctate (10–15 µm / confluent–1), interspaces shiny; marginal zones wide, equal to length of discs. Pseudopygidial area narrow, linear. Pygidial plate trapezoidal, apically truncate. Processes on sides of S6 normal, with short projections. Metasomal terga and sterna with punctures more or less equally dense (Fig. 5D).



Figure 4. *Epeolus rasmonti* Astafurova & Proshchalykin, sp. nov., holotype, female, habitus, lateral view. Scale bar: 1.0 mm.

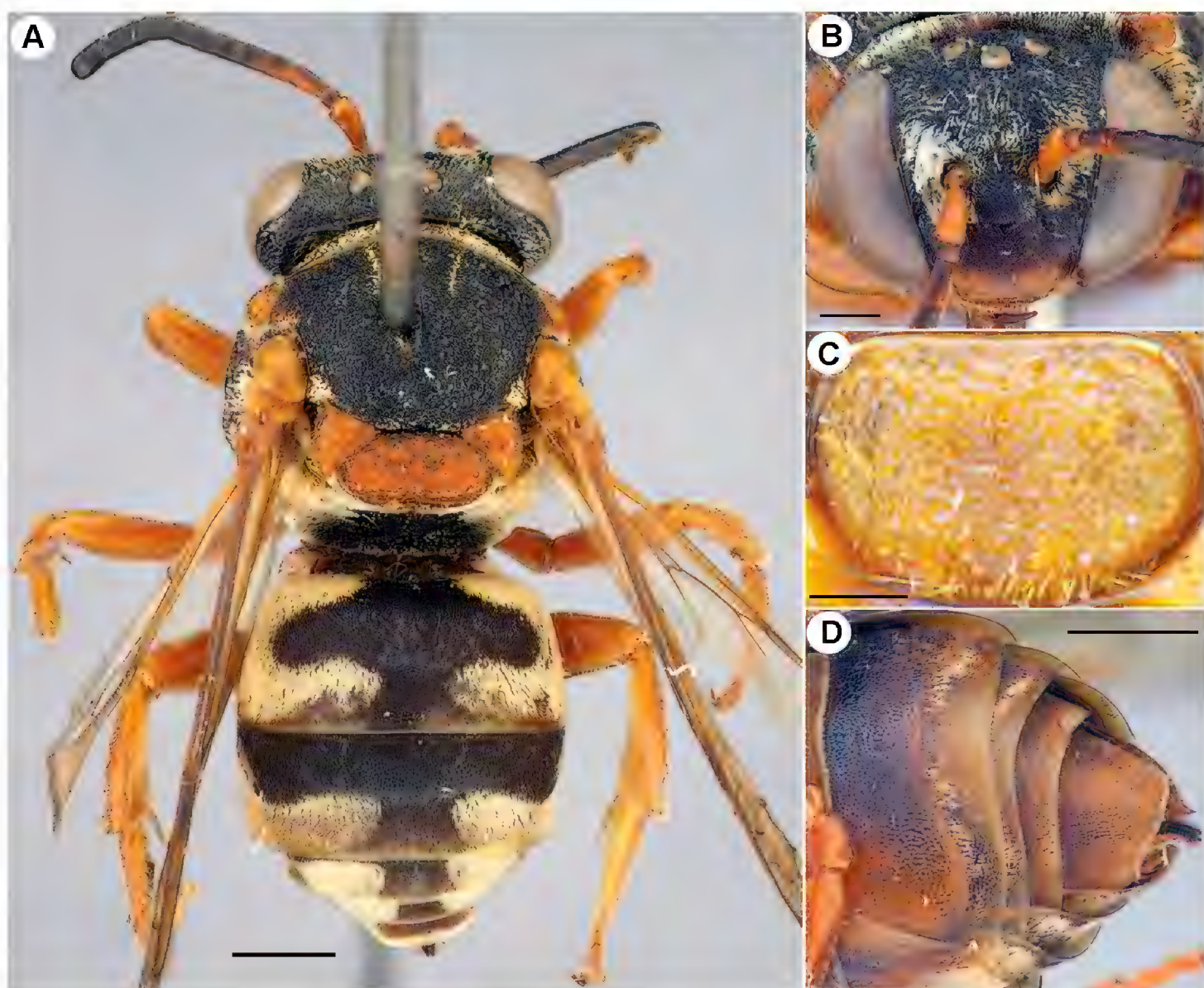


Figure 5. *Epeolus rasmonti* Astafurova & Proshchalykin, sp. nov., holotype, female **A** habitus, dorsal view **B** head, frontal view **C** labrum, frontal view **D** metasoma, ventral view. Scale bars: 1.0 mm (**A**, **D**); 0.5 mm (**B**); 0.3 mm (**C**).

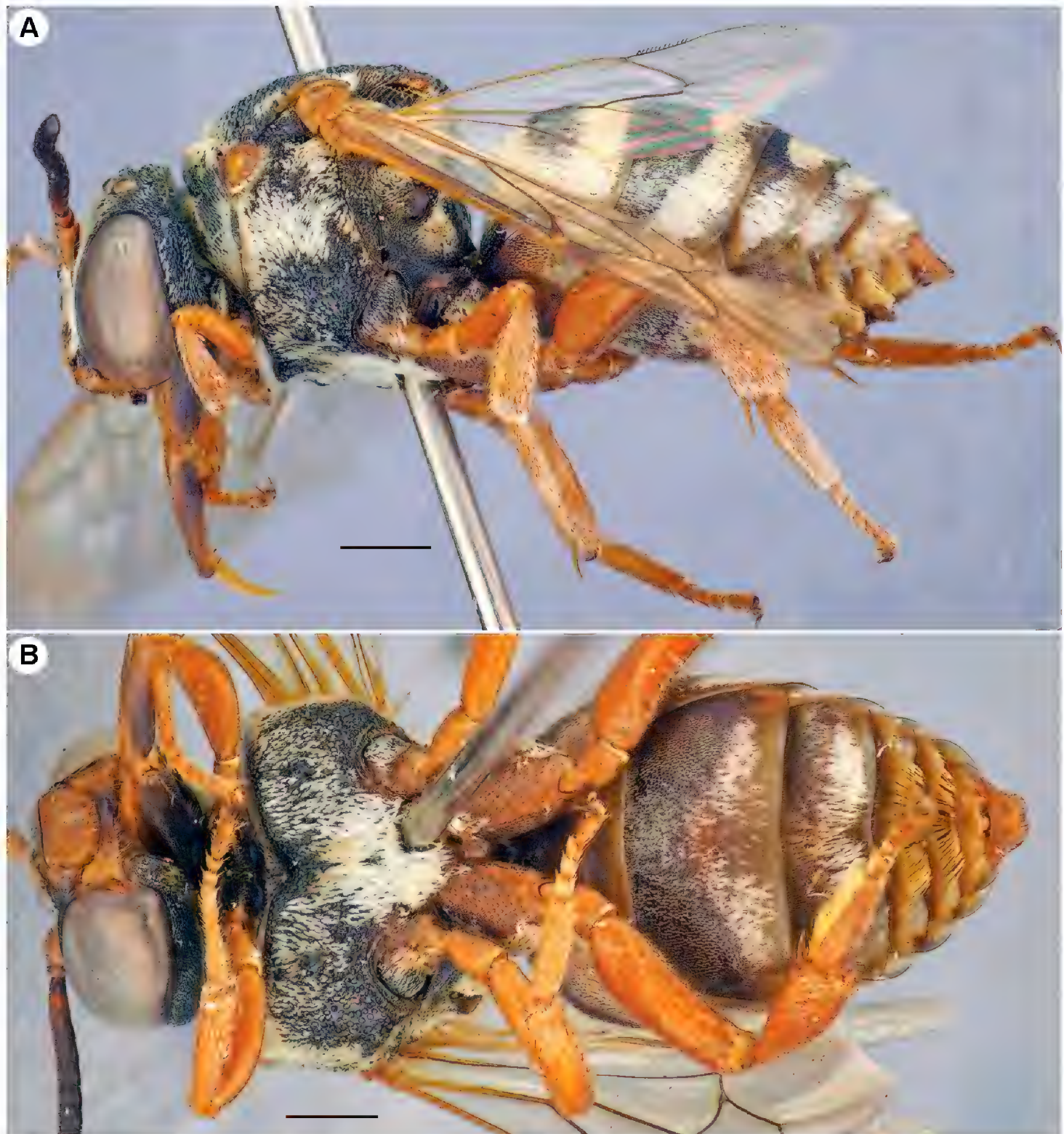


Figure 6. *Epeolus rasmonti* Astafurova & Proshchalykin, sp. nov., paratype, male **A, B** habitus, lateral view (**A**) ventral view (**B**). Scale bars: 1.0 mm.

Integument coloration: Head mostly black, but mandibles (excluding darker apex), labrum, clypeus along apical margin, scape and F1 reddish (amber). Mesosoma mostly black; pronotal lobe, tegulae, axillae, mesoscutellum, metanotum medially and legs (including spurs) reddish (amber); wings with brownish darkening, stigma and veins brown. Mesepisternum partially reddish (usually in middle part, lower scobal area). Metasomal terga black; marginal zones brownish to dark-golden apically. Pygidial plate reddish with brownish edging. Sterna brownish to reddish; margins golden.

Pubescence: Body with relatively sparse pubescence; tomentum white, except black on tergal discs. Labrum with thin sparse setae. Paraocular area with dense tomentum

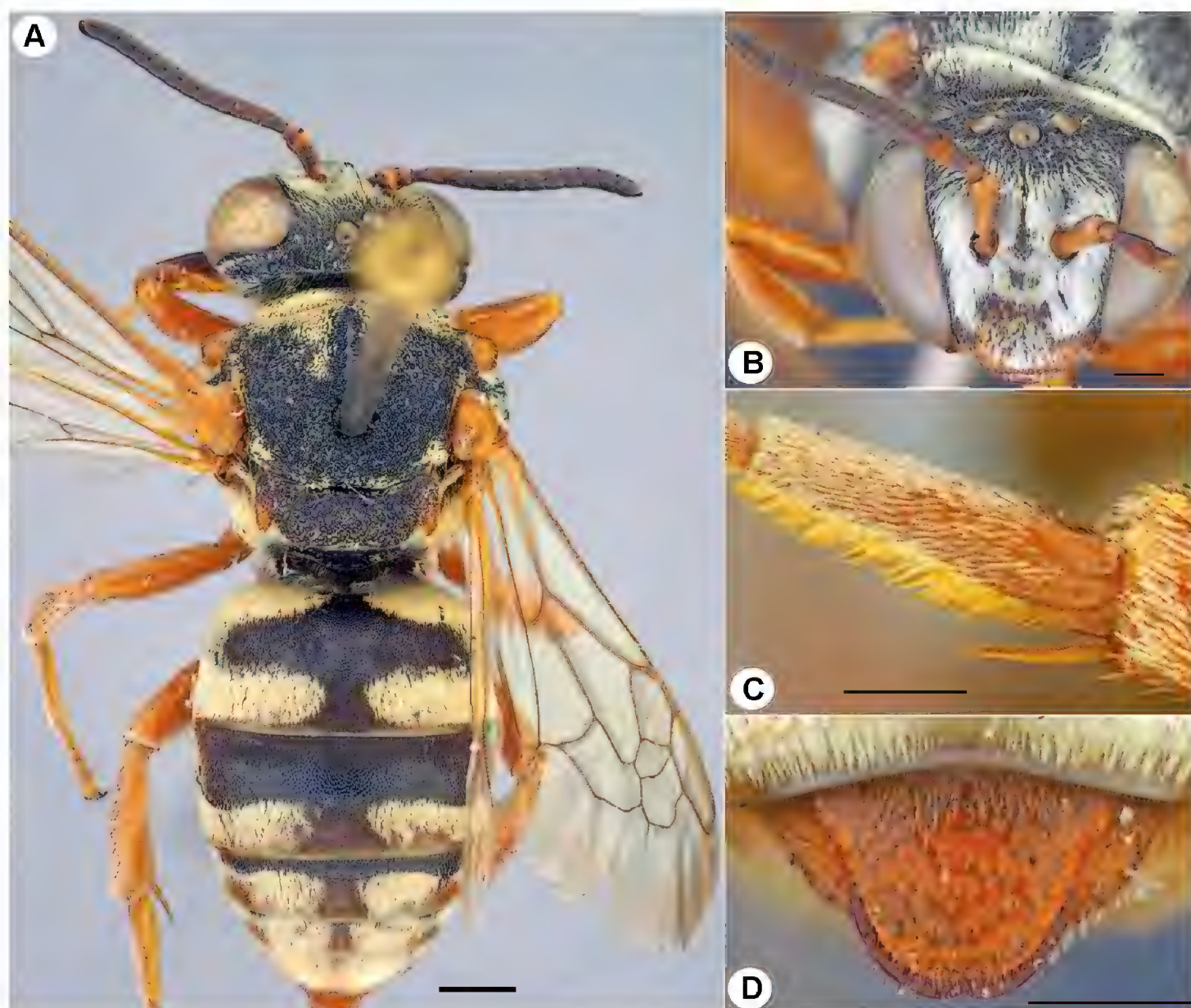


Figure 7. *Epeolus rasmonti* Astafurova & Proshchalykin, sp. nov., paratype, male **A** habitus, dorsal view **B** head, frontal view **C** hind basitarsus, dorsal view **D** T7, dorsal view. Scale bars: 1.0 mm (**A**); 0.5 mm (**B–D**).

obscuring integument; remaining part of face and vertex with sparse thin pubescence. Upper half of frons with relatively long erect simple setae mixed with adpressed sparse plumose pubescence. Genal area with relatively dense plumose setae, but not obscuring integument. Pronotum dorsally with tomentum obscuring integument, but medially setae sparse and short. Mesoscutum with dense tomentum peripherally and with narrow paramedial strips. Mesepisternum with sparse, short plumose pubescence or glabrous on lower part and with relatively dense and longer plumose pubescence on upper half. Metanotal integument obscured by tomentum except medially. Legs with sparse pubescence. T1 with basal band of tomentum interrupted medially and connected with apical band laterally; margins of T1–T4 with widely interrupted bands of tomentum. Black tomentum on T1–T4 discs and in interrupted area sparser than pale tomentum. T5 obscured by white tomentum laterally and black medially. Pseudopygidial area with white pubescence. Discs of metasomal sterna with short brownish plumose setae, sparse on S2 and entirely obscured by tomentum on S3–S5; margins with dense and pale tomentum interrupted medially.

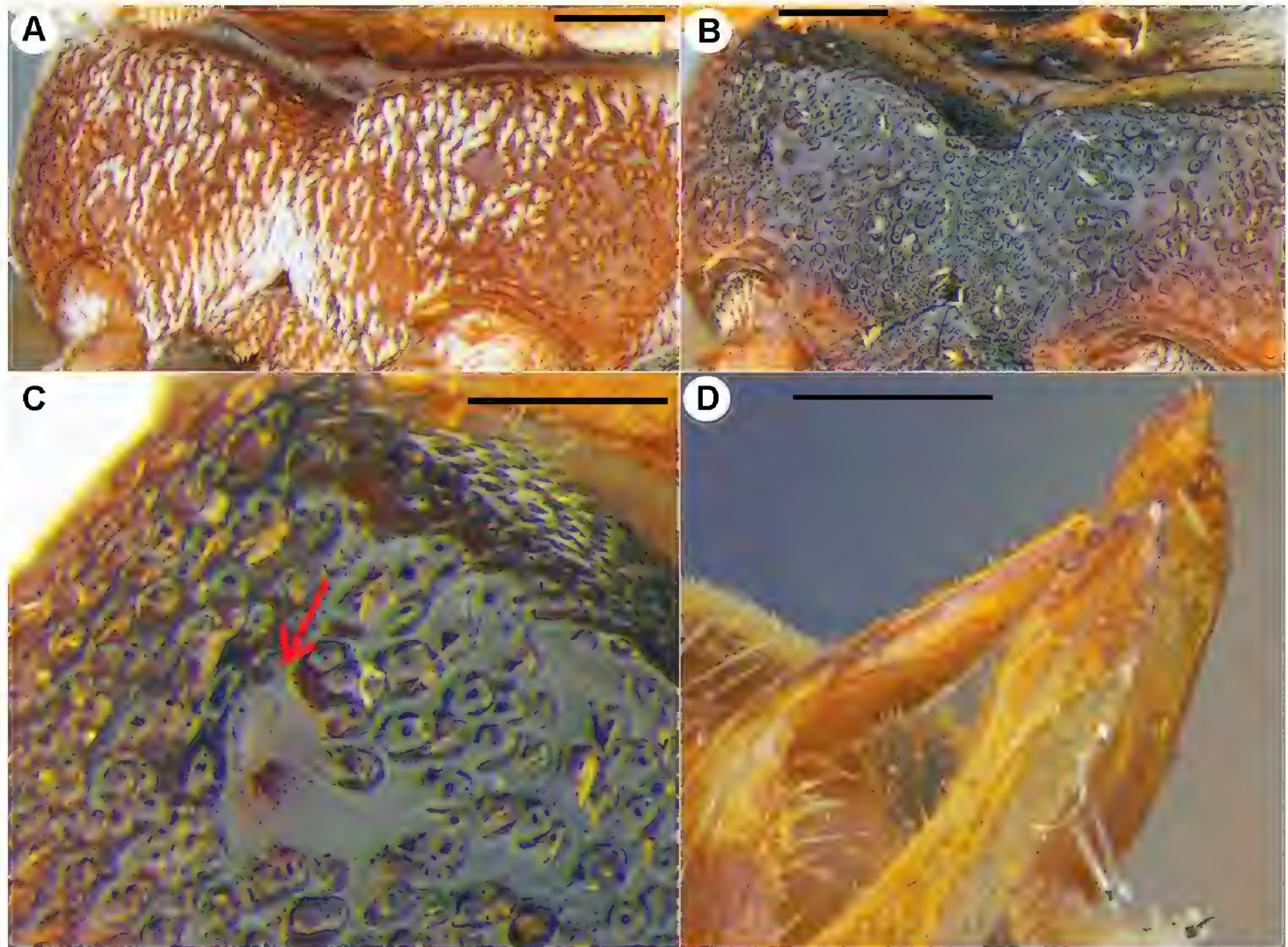


Figure 8. *Epeolus transitorius* Eversmann, 1852, female (**A**), *E. rasmonti* Astafurova & Proshchalykin, sp. nov., paratype, female (**B**, **C**), *E. kyzylkumicus* Astafurova, sp. nov., female (**D**) **A**, **B** lower mesepisternum, ventral view **C** subpleural signum (arrow), ventral view **D** S6, lateral view. Scale bars: 0.5 mm (**A**, **B**); 0.3 mm (**C**, **D**).

Male. Structure, sculpture, coloration and are similar to those of the female (Figs 6, 7), but pubescence more developed. Total body length 5.5–8.0 mm; forewing length (without tegula) 6.0–6.5 mm. F1 1.3–1.4 times as long as wide, succeeding flagellomeres ca 1.1 times as long as wide. Labrum with dense, plumose setae medially. Face obscured by plumose tomentum, but on upper frons sparser and mixed with long setae (Fig. 7B). Mesoscutum with paramedial strips wider than in female. Axillae and mesoscutellum black or reddish. Mesepisternum mostly areolate-punctate, with shiny, smooth interspaces on lower part; entirely obscured by tomentum. Hind basitarsus boarded by dense fringe of long golden setae (Fig. 7C). Metasomal terga with apical bands narrower interrupted than in female. Pygidial plate (T7) reddish, shiny, coarsely and densely punctate, ca 1.2 times wider than long, narrowed toward apex; apical margin rounded, slightly bilobed or almost straight (Fig. 7D). Margins of S2 and S3 with dense uninterrupted white tomentum bands; S4 and S5 normal, with gold long setae. Genitalia as on Fig. 9G, H.

Etymology. The specific epithet is a patronym honoring our colleague and friend Prof. Pierre Rasmont (University of Mons, Belgium) on the occasion of his 65th birthday and in recognition of his many contributions to the study of bee diversity.

Distribution (Fig. 10). Russia (Buryatia Rep.), Mongolia (Bulgan, Dornod, Khentii, Sukhbaatar), China (Beijing).

***Epeolus seraxensis* Radoszkowski, 1893**

Fig. 9A, B

Epeolus transitorius var. *seraxensis* Radoszkowski, 1893: 54–55, ♀, ♂ (lectotype: ♀, designated by Bogusch 2021: 59, Serax, Turkmenistan; Natural History Museum, Berlin).

Material examined. AZERBAIJAN, Araxesthal [=Nakhchivan Republic, near Ordubad], (1 ♀), Reitter leg. [ZISP]; KAZAKHSTAN, Tartugay, 3–15.VI.1929, (3 ♀, 2 ♂), A. Shestakov [ZISP]; Charyn valley, W Chundza, 650 m, 43°37'N, 79°21'E, 29–31.V.2001, (2 ♀), M. Hauser [OLBL]; 30 km ENE Shelek, 43°41.24'N, 78°38.50'E, 500 m, on Tamarix sp., 2.VIII.2002, (1 ♂), M. Kuhlmann [OLBL]; 3 km NE Boradysu, 30 km E Shelek, 19.VI.2003, (1 ♀), V. Kazenas [ZISP]; Charyn valley, 12 km W Chundzha, 12.VI.2004, (1 ♀, 1 ♂), V. Kazenas [ZISP]; TAJIKISTAN, Dushanbe, 1931, (1 ♀, 1 ♂), N. Fursov [ZISP]; TURKMENISTAN, Kopetdag, 12 km SW Kyzyl-Arvat, 24.V.1953, (1 ♂), Odintzova [ZISP].

Distribution. Azerbaijan, *Kazakhstan, *Tajikistan, Turkmenistan, Iran, Israel (Bogusch 2021; current records).

Remarks. Records from Bogusch (2021: 59) from Iran (“Anaesthal”) belong to specimens collected in Araxesthal, Azerbaijan, near Ordubad (see, Reitter 1890, 1905).

Variability. Females have well developed red body coloration, including the labrum, clypeus, pronotal lobe, tegulae, mesepisternum, axillae, mesoscutellum, metanotum, legs, pygidial plate and sterna. The antennae are brownish with the scape, pedicel and F1 entirely reddish. The mesoscutum is mostly black, sometimes with small red patterning peripherally and a pair red stripes posteriorly. The propodeum varies from entirely reddish to entirely black. The tergal discs vary from brownish to reddish. The males are mostly black, except the red labrum, scape, pedicel, F1, pronotal lobe, tegulae, legs and pygidial plate. The axillae and mesoscutellum are black or red. Tergal discs vary from black to brownish, and sterna from brownish to reddish.

***Epeolus siculus* Giordani Soika, 1944**

Epeolus siculus Giordani Soika, 1944: 20, ♀ (type locality: Messina, Sicily, Italy; holotype is lost).

Material examined. ITALY, Sicilia, (2 ♀), coll. F. Morawitz [ZISP]; Sicilia, 35 km SW Ragusa, 18–22.VI.2002, (1 ♂), J. Halada (OLBL).

Distribution. Italia (Sicilia) (Giordani Soika 1944).



Figure 9. Male, genitalia **A, C, E, G, I** genital capsule, dorsal view **B, D, F, H, J** penis, dorsal view **A, B** *Epeolus seraxensis* Radoszkowski, 1893 **C, D** *Epeolus kyzylkumicus* Astafurova, sp. nov. **E, F** *E. julliani* Pérez, 1884 **G, H** *E. rasmonti* Astafurova & Proshchalykin, sp. nov. **I, J** *E. laticauda* Bischoff, 1930. Scale bars: 0.5 mm.

Epeolus transitorius Eversmann, 1852

Figs 8A, 10

Epeolus transitorius Eversmann, 1852: 102 (lectotype: ♀, designated by Le Divelec 2021: 16, Indersk District, Atyrau Province, Kazakhstan; ZISP).

Material examined. GEORGIA, Tiflis[=Tbilisi], (1 ♀), coll. F. Morawitz, *transitorius* Eversm. [Morawitz det.] [ZISP]; KAZAKHSTAN, Zaysan, IX.1908, (1 ♂), coll. Gussakovskij [ZISP]; Fort Aleksandrovsk[=Fort-Shevchenko], 5.VII.1909, (1 ♂), Nasonov [ZISP]; Berchogur[=Birshoghyr], 26.VI.1910, (1 ♂), L. Bubyer [ZISP]; Chernoretsk, 11.VII.1925, (2 ♂), coll. Gussakovskij [ZISP]; near Chelkar Lake, Bolshiye Barsuki desert, 20.VI–10.VII., (1 ♀) [ZMMU]; Yanvartsevo, 19.VI–17.VIII.1950, (1 ♀, 5 ♂), V. Rudolf [ZISP]; 10 km N Zharkol Lake, 9.VII.1950, (2 ♀), V. Rudolf [ZISP]; Tengiz Lake, 3.VII.1957, (2 ♂), V. Rudolf [ZISP]; Kokshetau, on *Allium glabrosum*, 11.VII.1958, (1 ♀), V. Rudolf [ZISP]; 50 km E Balkhash Lake, 26–27.VI.1992, (1 ♀, 2 ♂), J. Halada [OLBL]; 5 km W Shardara, 250 m, 41°16'N, 67°53'E, 23–24.V.2016, (1 ♀, 1 ♂), J. Halada [OLBL]; RUSSIA, Astarakhan Prov., 35 km NNE of Astrakhan, 26.VII.2015, (1 ♀, 6 ♂), MP, VL, S. Belokobylskij, M. Mokrousov [ZISP]; Altai Terr., Novovoznesenka, 11.VII.1922, (2 ♂), A. Reygardt [ZISP]; CRIMEA, 8 km N of Dmitrovka, 5.VI.2018, (1 ♀), V. Savchuk [ZISP]; Mirny, Donuslav Lake, 17.VII.2017, (1 ♀), AF [ZISP]; Dagestan Rep., 20 km W of Makhachkala, Sarykum, 20–29.V.2019, (2 ♀, 1 ♂), MP, VL [FSCV]; Kalmykia Rep., 22 km E of Yashkul, 16–18.VII.2015, (1 ♀, 2 ♂) MP, VL, S. Belokobylskij, M. Mokrousov [FSCV/ZISP]; 17 km SWW of Artezian, Kuma River, 18–24.VII.2015, (2 ♀, 9 ♂), MP, VL, S. Belokobylskij, M. Mokrousov [FSCV/ZISP]; Orenburg Prov., Mayachnaya, 4.VIII.1993, (1 ♀), L. Zimin [ZMMU]; Orenburg, 9.VIII–3.IX.1926, (6 ♀, 1 ♂), P.A. Vorontzovskiy [ZISP]; Volgograd Prov., Sarepta, (2 ♀, 2 ♂), coll. F. Morawitz [ZISP]; Tinguta, 11.VIII.1952, (2 ♂), G. Viktorov [ZMMU]; TAJIKISTAN, Yagnob River, (1 ♂), coll. F. Morawitz, *transitorius* Eversm. [Morawitz det.] [ZISP]; Stalinabad[=Dushanbe], 18.VII.1936, (2 ♀), VG [ZISP]; idem, 15.VII.1943, (2 ♀, 1 ♂), V. Popov [ZISP]; UKRAINE, Yareski, 21.VII.1922, (2 ♀), coll. V. Gussakovskij [ZISP]; Kharkov, (1 ♂), coll. F. Morawitz, *transitorius* Eversm. [Morawitz det.] [ZISP]; UZBEKISTAN, Kurgan-Tyube[=Kurgantepa], Fergana, 27.V., 17.VII.1938, (1 ♀, 1 ♂), V. Popov [ZISP].

Variability. Females typically have well developed red body coloration. The labrum, pronotal lobe, tegulae, metanotum (medially), legs, and sterna are always red. The clypeus is usually red, but rarely can be mostly black or dark brownish (except with a red apical margin). The antennae are typically brownish with a red scape, pedicel and F1. The pronotum varies from black to partially red. The mesoscutum is mostly black, but red patterning sometimes also occurs laterally. Coloration of the mesepisternum varies from entirely red to partially black. The axillae and mesoscutellum are usually red, but rarely black peripherally. The terga are black or brownish, but T5 apically is typically red; sometimes red patterning occurs also on the anterior half of T1 and along margins. Pubescences of female is moderate. The face (except upper half of frons) is often obscured by dense tomentum, but 45% of specimens examined have the clypeus with sparse pubescence or almost glabrous. The mesepisternum is densely tomentose on the upper half and with sparse pubescence or glabrous below the scobal suture.

The males do not show significant variability. The body is mostly black, but the labrum, scape, pedicel, pronotal lobe, tegulae, legs and pygidial plate are red. The clypeus is black or with red patterning apically. The axillae and mesoscutellum are

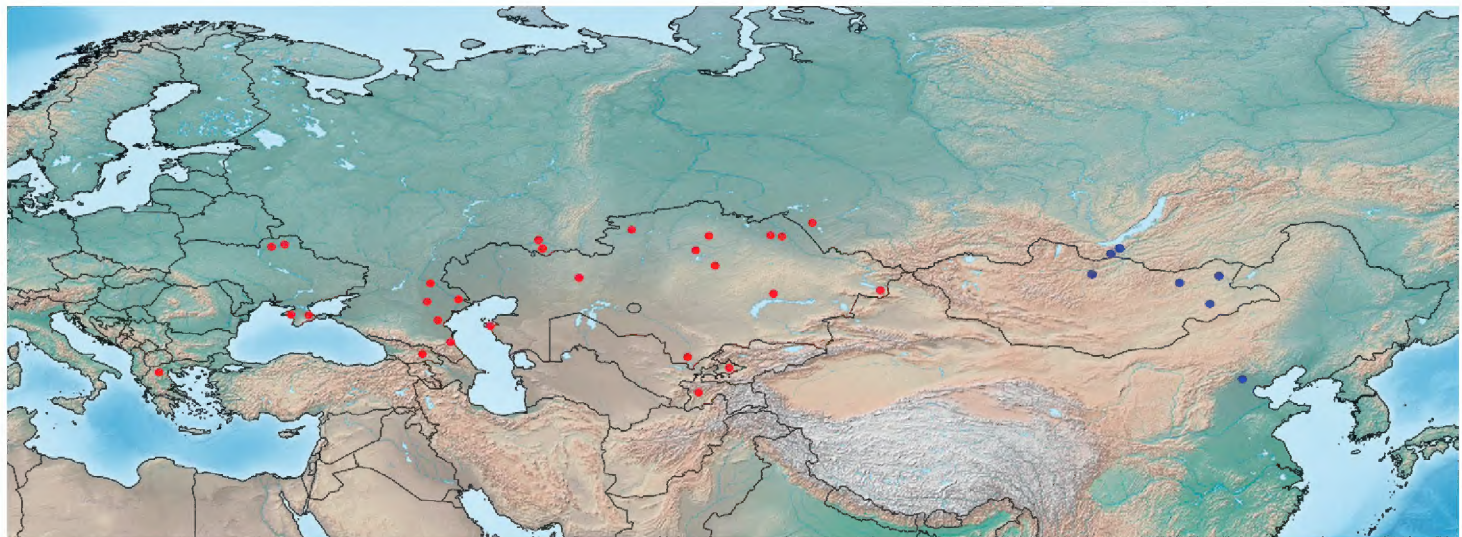


Figure 10. Distribution of *Epeolus transitorius* Eversmann (red dots) and *E. rasmonti* Astafurova & Proshchalykin, sp. nov. (blue dots).

usually black, often with red axillar teeth, sometimes partially red on mesoscutellum. The sterna are black or brownish to red along margins; marginal zones are golden. The pygidial plate is apically rounded, sometimes more or less straight or slightly bilobed.

Distribution (Fig. 10). Greece, Georgia, Ukraine, Russia (south of European part, south Ural, SW Siberia), Kazakhstan, Uzbekistan, Tajikistan (Le Divelec 2021; current data).

Remarks. The previous records of *Epeolus transitorius* from North Africa, Europe, Caucasus and Iran (Fries 1893, 1895; Bischoff 1930; Popov 1967; Bogusch and Hadrava 2018; Bogusch 2021) are mostly wrong (see Le Divelec 2021). Records from Morawitz (1875: 144, from Tajikistan [=Levchenko et al. 2017: 317, as Uzbekistan]) belongs to *E. michailovi* Astafurova & Proshchalykin, 2021; records from Turkmenistan (Levchenko et al. 2017: 317) refer to *E. seraxensis* Radoszkowski, 1893.

Discussion

The *Epeolus julliani* species group is distributed only in the southern Palearctic, ranging from northern Africa to China. Eight of the nine species occur in the Western Palearctic, and only *Epeolus rasmonti* sp. nov. is known only from the Eastern Palearctic. There are no species with a Trans-Palearctic range. *Epeolus julliani* is the most widespread species in this group, occurring from North Africa and Southern Europe east to the Middle East and Central Asia and north to the Urals. *Epeolus transitorius* occurs from Eastern Europe and Central Asia to Western Siberia. *Epeolus seraxensis* is distributed from the Middle East and Caucasus to Central Asia. *Epeolus fasciatus* Fries, 1895 occurs from Southern Europe to Turkey. The remaining species are endemics—*Epeolus siculus* – Sicily; *E. laticauda* Bischoff, 1930 and *E. kyzylkumicus* sp. nov. – Central Asia; *E. iranicus* – Iran.

Species of the group do not demonstrate as much intraspecific variation as has been observed within those in the *E. cruciger* species group (Astafurova and Proshchalykin

2022). The main combination of features to distinguish species in the *julliani* group is coloration and pubescence of the body, length of flagellomeres, and shape/width of the male pygidial plate (Table 1). The shape of the lateral lobes of the penis is an additional feature that can reliably distinguish species in this group (Fig. 9).

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References

- Astafurova YuV, Proshchalykin MYu (2021a) Review of the *Epeolus tarsalis* species group (Hymenoptera: Apidae, *Epeolus* Latreille, 1802), with description of a new species. *Zootaxa* 5006(1): 26–36. <https://doi.org/10.11646/zootaxa.5006.1.6>
- Astafurova YuV, Proshchalykin MYu (2021b) New and little-known bees of the genus *Epeolus* Latreille, 1802 (Hymenoptera, Apidae, Nomadinae) from Mongolia. *Journal of Hymenoptera Research* 84: 11–28. <https://doi.org/10.3897/jhr.84.67150>
- Astafurova YuV, Proshchalykin MYu (2021c) A new species of the genus *Epeolus* Latreille, 1802 (Hymenoptera, Apoidea: Apidae) from the Pamirs, with a checklist of Central Asian species. *Far Eastern Entomologist* 437: 10–15. <https://doi.org/10.25221/fee.437.3>
- Astafurova YuV, Proshchalykin MYu (2022) Review of the *Epeolus cruciger* species group (Hymenoptera: Apidae, *Epeolus* Latreille, 1802) of Asia, with the description of two new species. *Journal of Hymenoptera Research* 92: 305–328. <https://doi.org/10.3897/jhr.92.90098>
- Bischoff H (1930) Beitrag zur Kenntnis palaarktischer Arten der Gattung *Epeolus*. *Deutsche entomologische Zeitschrift* 1930: 1–15. <https://doi.org/10.1002/mmnd.193019300102>
- Bogusch P (2018) Three new species and new records of cuckoo bees of the genus *Epeolus* in Turkey (Hymenoptera: Apidae: Nomadinae). *Acta Entomologica Musei Nationalis Pragae* 58: 127–135. <https://doi.org/10.2478/aemnp-2018-0010>
- Bogusch P (2021) The cuckoo bees of the genus *Epeolus* Latreille, 1802 (Hymenoptera, Apidae) from the Middle East and North Africa with descriptions of two new species. *Journal of Hymenoptera Research* 84: 45–68. <https://doi.org/10.3897/jhr.84.67049>
- Bogusch P, Hadrava J (2018) The bees of the genera *Epeolus* Latreille, 1802 and *Triepeolus* Robertson, 1901 (Hymenoptera: Apidae: Nomadinae: Epeolini) of Europe: taxonomy,

- identification key, distribution, and ecology. *Zootaxa* 4437(1): 1–60. <https://doi.org/10.11646/zootaxa.4437.1.1>
- Engel MS (2001) A monograph of the Baltic amber bees and evolution of the Apoidea (Hymenoptera). *Bulletin of the American Museum of Natural History* 259: 1–192. [https://doi.org/10.1206/0003-0090\(2001\)259<0001:AMOTBA>2.0.CO;2](https://doi.org/10.1206/0003-0090(2001)259<0001:AMOTBA>2.0.CO;2)
- Eversmann E (1852) Fauna hymenopterologica volgo-uralensis (Continuatio). *Bulletin de la Société impériale des Naturalistes de Moscou* 25(2/3): 3–137.
- Friese H (1893) Die Bienenfauna von Deutschland und Ungarn. R. Friedlander & Sohn, Berlin, 79 pp.
- Friese H (1895) Die Bienen Europa's (Apidae europaeae) nach ihren Gattungen, Arten und Varietäten auf vergleichend morphologisch-biologischer Grundlage. Theil I: Schmarotzerbienen R. Friedländer, Berlin, 218 pp. <https://doi.org/10.5962/bhl.title.160173>
- Giordani Soika A (1944) Contributo alla conoscenza dei Vespidi solitari e sociali della regione etiopica. *Atti del Regio Istituto Veneto di Scienze* 103: 149–178.
- Latreille PA (1802) Histoire naturelle, generale et particuliere, des Crustaces et des Insectes. *Historie naturelle des Crustaces et des Insectes* 3: 1–467. <https://doi.org/10.5962/bhl.title.15764>
- Le Divelec R (2021) The West Palaearctic Epeolini Linsley & Michener, 1939 housed in the Muséum national d'Histoire naturelle (Paris) with some taxonomic notes (Hymenoptera: Apidae: Nomadinae). *Annales de la Société entomologique de France (N.S.)* 57(4): 313–345. <https://doi.org/10.1080/00379271.2021.1942206>
- Lim K, Lee S, Orr M, Lee S (2022) Harrison's rule corroborated for the body size of cleptoparasitic cuckoo bees (Hymenoptera: Apidae: Nomadinae) and their hosts. *Scientific Reports* 12: 10984. <https://doi.org/10.1038/s41598-022-14938-9>
- Levchenko TV, Byvaltsev AM, Proshchalykin MYu (2017) Family Apidae. In: Lelej AS, Proshchalykin MYu, Loktionov VM (Eds) *Annotated Catalogue of the Hymenoptera of Russia. Volume I. Symphyta and Apocrita: Aculeata. Proceedings of the Zoological Institute RAS, Supplement 6*: 263–276.
- Michener CD (1944) Comparative external morphology, phylogeny, and a classification of the bees. *Bulletin of the American Museum of Natural History* 82: 151–326.
- Michener CD (2007) *The Bees of the World* (2nd edn.). Johns Hopkins University Press, Baltimore, 953 pp. [+ 20 pls] <http://base.dnsgb.com.ua/files/book/Agriculture/Beekeeping/Thep-Bees-of-the-World.pdf>
- Morawitz F (1875) A travel to Turkestan by the member-founder of the society A. P. Fedtschenko, accomplished from the Imperial Society of Naturalists, Anthropologists, and Ethnographers on a Commission from the General-Governor of Turkestan K. P. von Kaufmann (Issue 9). Vol. II. Zoogeographical Investigations. Pt. V. (Division 7). Bees (Mellifera). Pt. I [Apidae genuinae]. *Izvestiya Imperatorskogo Obshchestva Lyubiteley Estestvoznaniya, Anthropologii i Ethnografii* 21(3): 1–160. [in Russian]
- Onuferko TM, Bogusch P, Ferrari R, Packer L (2019) Phylogeny and biogeography of the cleptoparasitic bee genus *Epeolus* (Hymenoptera: Apidae) and cophylogenetic analysis with its host bee genus *Colletes* (Hymenoptera: Colletidae). *Molecular Phylogenetics and Evolution* 141: e106603. <https://doi.org/10.1016/j.ympev.2019.106603>

- Pérez J (1884) Contribution a la faune des Apiaires de France. Actes de la Société linnéenne de Bordeaux 37: 257–378.
- Popov VB (1935) Contributions to the bee fauna of Tajikistan (Hymenoptera, Apoidea). Trudy Tajikskoi Basy Akademii Nauk SSSR 5: 351–408. [in Russian]
- Popov VB (1949) Notes on the bee fauna of Tajikistan (Hymenoptera, Apoidea). Trudy Zoologicheskogo Instituta Akademii Nauk SSSR 8: 688–699. [in Russian]
- Popov VB (1967) The bees (Hymenoptera, Apoidea) of Middle Asia and their associations with angiosperm plants. Trudy Zoologicheskogo Instituta Akademii Nauk SSSR 38: 11–329. [in Russian]
- Radoszkowski O (1893) Faune hyménoptérologique transcaspienne. (Suite et Fin). Horae Societatis Entomologicae Rossicae 27(1/2): 38–81.
- Reitter E (1890) Eine neue mit *Athous* verwandte Elateriden. Gattung aus russisch Armenien. Entomologische-Nachrichten 16: 247–248.
- Reitter E (1905) Neun neue Coleopteren aus der palaearktischen Fauna. Wiener Entomologische Zeitung 24(5–6): 201–206.
- Shorthouse DP (2010) SimpleMappr, an online tool to produce publication-quality point maps. <https://www.simplemappr.net/> [accessed 12 October 2022]